Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA

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ABSTRACT: We compared densities of nekton and infauna among 5 natural and 10 created (3 to 15 yr in age) salt marshes in the Galveston Bay system of Texas to test whether these marshes were functionally equivalent. Decapod crustaceans dominated the nekton on the marsh surface during both the spring and the fall. Densities of daggerblade grass shrimp *Palaemonetes pugio*, the most abundant decapod, were not significantly different among marshes, but the size of these shrimp in created marshes was significantly smaller than in natural marshes. Densities of the marsh grass shrimp *Palaemonetes vulgaris* and of 3 commercially-important crustaceans (white shrimp *Penaeus setiferus*, brown shrimp *Penaeus aztecus*, and blue crab *Callinectes sapidus*) were significantly lower in created marshes than in natural marshes. Gulf menhaden *Brevoortia patronus* were the most abundant fish collected, mainly on nonvegetated bottom adjacent to marsh habitats. Fish densities within vegetation (predominantly gobies and pinfish *Lagodon rhomboides*) were significantly lower in created marshes than in natural marshes. Natural and created marshes, however, did not differ in species richness of nekton. Sediment macro-organic matter and density and species richness of macroinfauna (mainly polychaete worms) were all significantly lower in created marshes than natural marshes. There was a positive relationship in created marshes between marsh age and sediment macro-organic matter, but marsh age was not related to nekton densities. Natural marshes were similar in having low elevations and flooding durations between 74 and 80% of the year; while created marshes were flooded from 43 to 91% of the time. In contrast to marsh age, tidal flooding was often related to nekton densities in marsh habitats. We conclude that marsh elevation and tidal flooding are key characteristics affecting use by nekton and should be considered in marsh construction projects.

KEY WORDS: Salt marsh · Habitat value · Habitat creation · Restoration · Nekton · Fishery species

INTRODUCTION

The northern Gulf of Mexico is characterized by vast expanses of estuarine wetlands and some of the most productive fisheries in the USA. Fishery productivity is closely linked to these wetlands, and both correlative (Turner 1977, Zimmerman & Minello 1984, Rozas & Reed 1993, Peterson & Turner 1994) and experimental (Minello & Zimmerman 1983, Minello et al. 1989, Thomas 1989, Minello & Zimmerman 1991, Heck &

Coen 1995) evidence indicates that many fishery species in the region depend upon coastal marshes for critical nursery functions such as provision of food for growth and protection from predators. Wetland loss in the region has encouraged efforts to restore salt marshes by planting smooth cordgrass *Spartina alterniflora* on eroding shorelines, graded-down uplands, or on deposits of dredged material. Although techniques are available for successfully establishing stands of this vegetation under various coastal conditions (Woodhouse et al. 1972, Broome et al. 1988, Broome 1989), the relative value of these created

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marshes for estuarine animals in relation to natural marshes is still a matter of controversy (Race & Christie 1982, LaSalle et al. 1991, Moy & Levin 1991, Simenstad & Thom 1996, Zedler 1996).

Created salt marshes are generally similar to natural marshes in physical appearance. Indeed, these marshes often appear more productive than natural marshes on the basis of above-ground plant biomass (Webb & Newling 1985, Broome 1989). However, accumulating evidence suggests that natural and created marshes are not functionally equivalent for nekton and other estuarine organisms (Moy & Levin 1991, Minello & Zimmerman 1992, Meyer et al. 1993, Zedler 1993, Havens et al. 1995, Zedler 1996). Therefore, replacement of natural marshes with created marshes may result in losses of estuarine and fishery productivity. We need better documentation of functional differences between these marsh types to assess the magnitude of these losses. In addition, if we assume that created marshes can eventually reach functional equivalence with natural marshes, we need information on the optimal conditions and projected time required for this development.

The objective of this study was to compare the relative value of created and natural salt marshes for nekton in the Galveston Bay system of Texas. We assumed marsh use was an indicator of habitat value and measured nekton densities in marshes with an enclosure device (Zimmerman et al. 1984). Five natural marshes were compared with 10 created marshes, ranging in age from 3 to 15 yr. We expected this age range to allow an assessment of functional development rate in created marshes. In association with nekton densities, we measured sediment macro-organic matter and the abundance of benthic infaunal organisms available as prey to nektonic predators. We also examined tidal flooding duration as a possible factor governing nekton use of the marshes.

METHODS

Study area. The Galveston Bay system is the largest estuary in Texas (1420 km^2). *Spartina alterniflora* is the dominant shoreline vegetation in the bay, and the young of many fishery species have been shown to directly utilize this intertidal habitat (Zimmerman & Minello 1984, Thomas et al. 1990). Due to coastal development, erosion, and subsidence, 19 to 20% of emergent marshes were lost in the bay system between 1950 and 1989 (White et al. 1993, White & Tremblay 1995).

Selection of marshes. We identified 10 created marshes that ranged in age from 3 to 15 yr at the time of sampling; substratum type and construction technique also differed among some marshes (Table 1). More detailed physical descriptions of the marshes are available in Delaney (1994). All marshes were distinct entities and separated by at least 0.5 km of nonvegetated shoreline. The created marshes were located along shorelines of channels, lakes, coves, or the open bay (Fig. 1), and the distance of shoreline covered by these marshes ranged approximately from 50 to 700 m. We selected natural marshes that were also located along shorelines, and the length of shoreline sampled for all marshes was less than 700 m. Natural marshes included 2 relatively large marshes, one at Jamaica Beach in West Bay (N4) and one at Peppergrove Cove on Bolivar Peninsula in East Bay (N1); these marshes have been described in previous studies (Zimmerman & Minello 1984, Webb & Newling 1985). We also included natural marshes along the Lake Como Channel (N3) and along the shoreline of Halls Lake (N5) because of their proximity to the created marshes T1 & T2. The Bolivar Shoreline marsh (N2) was on an exposed shoreline in East Bay and was selected because the high-energy conditions here were similar to those at transplanted marshes on Bolivar (T6, T7, T8, & T9).

Table 1. Basic information about created marshes used in this study. Creation technique: PL, planted; NR, naturally revegetated; substrate: DM, dredged material; NS, natural shoreline; GU: graded-down upland; age: marsh age in years at the time of sampling in 1990; location: center of marsh shoreline measured with a Global Positioning System receiver

| Created marsh	Creation technique	Substrate	Area (ha)	Age	Location Latitude (N)	Longitude (W)
T1 Alligator Point	PL	DM	10.5	7	29° 10' 38"	95° 06' 51"
T2 Lake Como	PL	GU	<0.1	5	29° 12' 23"	94° 57' 07"
T3 Palm Beach	PL	NS	<0.1	6	29° 16' 44"	94° 50' 57"
T4 Pelican Spit	PL	DM	1.2	3	29° 20' 52"	94° 49' 50"
T5 Little Pelican Isle	NR	DM	4.5	7	29° 20' 56"	94° 49' 32"
T6 Bolivar Floating Tires	PL	DM	<0.1	5	29° 24' 40"	94° 44' 35"
T7 Bolivar Islands	PL	DM	0.9	5	29° 24' 45"	94° 44' 29"
T8 Bolivar Revegetated Shoreline	NR	DM	0.2	6	29° 24' 49"	94° 44' 20"
T9 Bolivar Sandbag Marsh	PL	DM	1.4	13	29° 25' 08"	94° 43' 56"
T10 Anahuac Refuge	PL	NS	0.7	15	29° 33' 14"	94° 28' 59"
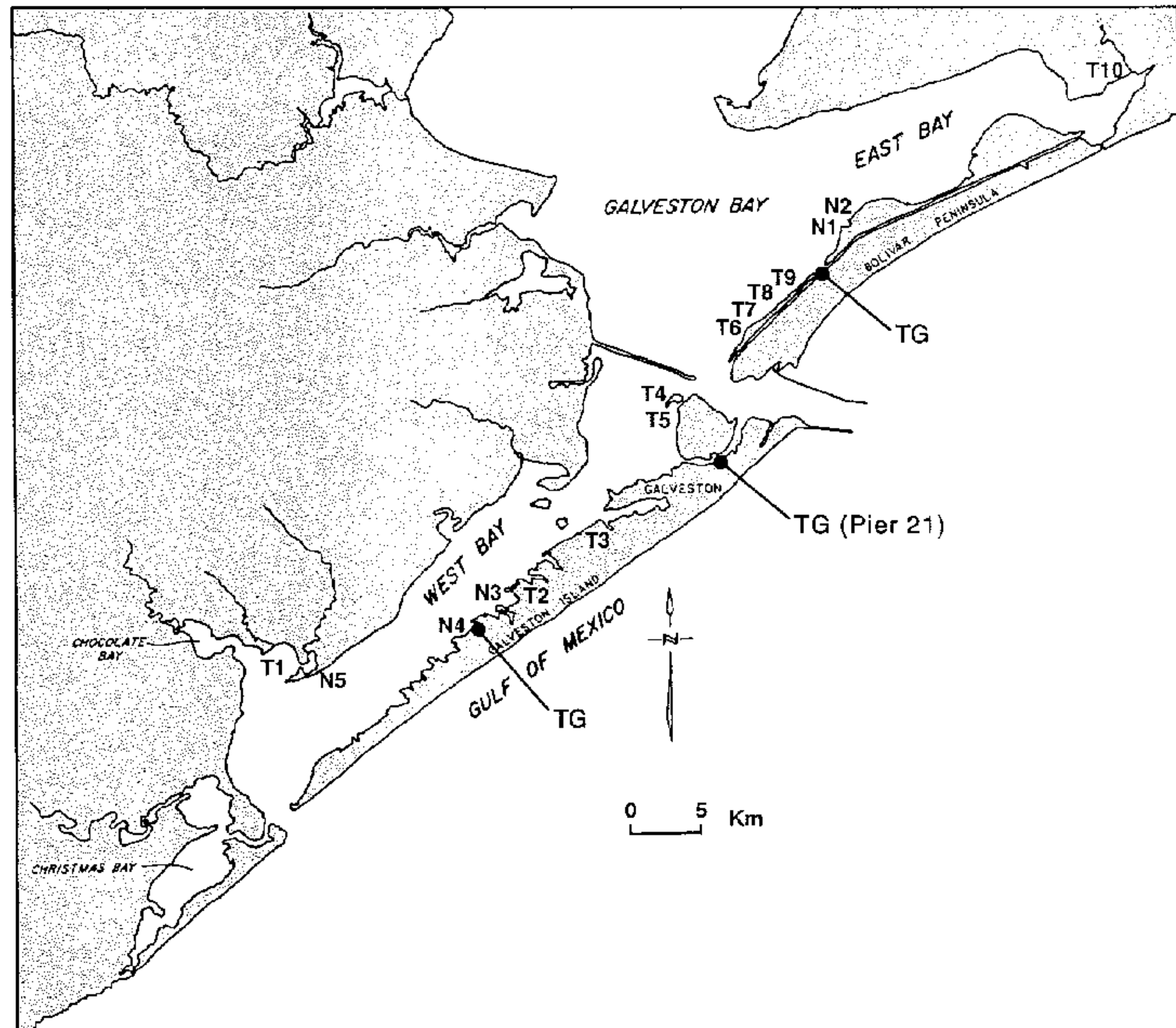
Fig. 1. Locations of natural (N1 to N5) and created (T1 to T10) *Spartina alterniflora* salt marshes in the Galveston Bay system of Texas. Locations of tide gauges (TG) are also shown

Habitats within each marsh. In each marsh, we collected nekton within 3 habitats: (1) the marsh edge (within *Spartina alterniflora* about 1 m from the marsh/water interface), (2) the inner marsh (about 5 m into the marsh), and (3) in subtidal habitat (the shallow nonvegetated bottom adjacent to the marsh). Inner marsh is a relative term, and others may consider it a misnomer for marsh habitat only 5 m from the open water. However, in many of the highly reticulated natural marshes of the lower bay, vegetation occurs as islands less than 10 m across; thus samples cannot be taken further than 5 m from a marsh/water interface. In addition, many of the created marshes in this study are narrow strips of vegetation fringing the shoreline, and some (such as the marsh at Palm Beach, T3) are not much wider than 5 m.

Sampling. We sampled nekton in fall 1990 (September 24 to 28) and spring 1991 (May 13 to 17). The T7 marsh was covered with dredged material from the Intracoastal Waterway between our sampling periods and was not sampled in spring 1991. The T6 & T8 marshes also were impacted by the dredging operation, and a thin layer (5 to 10 cm) of sediment was deposited over portions of these marshes. We restricted the collection of spring samples in these marshes to areas that did not appear to have any newly deposited sediment.

We estimated nekton densities using a drop sampling technique with a 1.8 m diameter cylinder as described by Zimmerman et al. (1984). We collected 6 drop samples (2 randomly located in each habitat) in each marsh during daylight hours at high tide. We dropped the sampler from a boom on the bow of a skiff and pushed it into the substrate to make a watertight seal. Once the sampler was in place, we measured temperature, salinity, turbidity, dissolved oxygen, and water depth as described by Minello & Zimmerman (1992). Vegetation in a sample was clipped at the marsh surface and removed to facilitate the collection of animals. We used dip nets to remove most enclosed fauna in the 2.6 m^2 sampler and then pumped water from the sampler through a 1 mm mesh plankton net. Animals were preserved in the field in 10% formalin with Rose Bengal stain.

We also collected a sediment core (10 cm diameter, 5 cm deep) from within each drop sample to estimate the density of benthic infauna and epifauna. The core was taken near the center of the sampler (between clumps of *Spartina alterniflora* in vegetated habitats) before the sediments were disturbed with dip nets. We washed the upper 5 cm of sediment through a 0.5 mm mesh sieve in the field and preserved animals and plant material (roots and detritus) in 10% formalin with Rose Bengal stain.

In the laboratory, we identified all fishes, crustaceans, and molluscs from drop samples. We measured total lengths for fishes and crustaceans (cara-

pace width for crabs) and recorded length data in 5 mm intervals for most species and 1 mm intervals for penaeid shrimp. Infaunal organisms from the sediment cores were separated from detritus and plant material, grouped into major phyla, and counted. We identified polychaetes and peracarid crustacea to species. Macro-organic matter (MOM) from sediment cores, which consisted of detritus and live below-ground plant material retained on the sieve, was dried at 100°C to a constant weight.

Marsh hydroperiod. Tidal flooding patterns were determined through the use of 3 recording water level gauges. Data were obtained from NOAA's National Ocean Service tide gauge at Pier 21 in the Galveston Channel (Station Number 877-1450), and we installed 2 temporary gauges, one in West Bay at Jamaica Beach and one in East Bay on Bolivar Peninsula (Fig. 1). These temporary gauges consisted of data loggers with pressure transducers located in PVC stilling wells, and they recorded water level every hour during part of the fall season in 1990 and throughout most of 1991. We estimated marsh surface elevations in relation to the nearest tide gauge for each nekton sample by comparing water depth measurements in the sampler with concurrent water level readings on the gauge. The flooding duration for each of these elevations was determined by recording the percentage of water-level records above that elevation on the gauge during any time period. Mean flooding durations in a marsh were calculated using these values plus other randomly collected estimates taken over the course of the study (between 13 and 22 observations per marsh).

Over the period from September 1, 1990 to August 31, 1991, our temporary gauges periodically malfunctioned (not during nekton sampling), and water level data were only available 68% of the time from the Jamaica Beach gauge and 58% of the time from the Bolivar gauge. Therefore, we used regression analyses to determine relationships between Pier 21 gauge data and the available data from our temporary gauges for the period from September 1990 through August 1991. The relationship for the Bolivar (BOL) gauge used a 2 h time lag (the tide reached Bolivar 2 h after Pier 21) and included 3834 data points; this regression (BOL = 30.095 + 0.368 Pier21 + 0.00168 Pier21^2) had an R^2 of 0.93. The relationship for the Jamaica Beach (JB) gauge employed a 3 h time lag and included 5350 data points; this regression (JB = 78.426 + 0.369 Pier21 + 0.00378 Pier21^2) had an R^2 of 0.90. These regressions were used to predict missing values on the temporary gauges for calculating flooding duration.

Statistical analysis. We used an analysis of variance (ANOVA) model to compare animal densities and other parameters among marshes during each season. A positive relationship between the mean and standard deviation for animal density data indicated that the ANOVA assumption of homogeneity of variances was not met, and a ln(y+1) transformation was used to correct this heteroscedasticity in the density data. The design was a completely randomized factorial model with Marsh (15 levels) and Habitat (nonvegetated, edge, inner marsh) as the main effects and with 2 replicates per treatment combination. A type I error of 0.05 or less was considered statistically significant. We partitioned the main effect of Marsh with *a priori* contrasts to compare natural and created marshes. Contrasts also were calculated within Marsh × Habitat interactions to compare natural and created marshes within habitats. For regression analyses, data from each drop sample were considered independent. We used simple linear regressions to examine the relationship between animal densities (transformed) on the marsh surface (subtidal data were excluded from these analyses) and the age of created marshes (n = 40 in fall and n = 36 in spring). Multiple regressions were calculated on data from all marshes to identify factors that might be important in determining the distribution of animals on the marsh surface; a forward stepwise selection technique was used with a partial F-ratio of 4.0 required to enter the model and of 3.996 for removal. Independent variables included annual flooding duration, sediment macro-organic matter, infauna density in sediment cores, sample water depth, water temperature, salinity, dissolved oxygen, and turbidity. Statistical analyses were conducted with SuperANOVA and StatView (Abacus Concepts, Inc., Berkeley, CA, USA, 1991).

RESULTS

Fishes

Fishes made up 5.4% of the fauna caught in the fall drop samples and 43.1% in the spring. Dominant species within marsh vegetation in the fall were the naked goby *Gobiosoma bosc* and darter goby *Gobionellus boleosoma* while the bay anchovy *Anchoa mitchilli* was abundant on subtidal nonvegetated bottom (Table 2). In the spring, gulf menhaden *Brevoortia patronus* dominated the samples (79.1% of all fish); these fish were found mainly in nonvegetated habitat. Pinfish *Lagodon rhomboides* and darter goby were abundant in vegetated samples.

There were small but significant differences in fish density between natural and created marshes. In the fall, overall fish densities were significantly higher in natural marshes (Table 3), but the difference in mean densities was only about 10% (Table 2). This difference was mainly due to densities in the inner marsh (Tables 2 & 3). In the spring, the overall mean density

Table 2. Mean densities and (in parentheses) standard errors of common macrofaunal organisms collected from 2.6 m^2 drop samples. Each habitat mean in natural marshes is from 10 samples; habitat means in created marshes are from 18 (spring) or 20 (fall) samples. Species were included if they made up >2% of fishes, crustaceans, or molluscs and are listed in order of their overall abundance within these groups. Mean sizes are in mm total length or carapace width

	Natural marshes				Created marshes			
	All habitats	Edge	Inner	Nonveg	All habitats	Edge	Inner	Nonveg
FALL 1990								
Total macrofauna	254.3 (48.75)	529.7 (88.35)	186.0 (37.53)	47.3 (7.52)	266.4 (51.26)	550.2 (127.83)	192.4 (34.67)	56.6 (9.73)
Fishes	15.2 (2.19)	16.7 (3.32)	10.1 (1.86)	18.9 (5.20)	13.7 (2.94)	20.9 (7.60)	6.2 (1.32)	14.1 (3.90)
Gobiosoma bosc	3.8 (1.08)	8.9 (2.51)	1.3 (0.62)	1.1 (0.46)	4.4 (1.77)	10.0 (5.06)	0.6 (0.31)	2.7 (0.91)
Anchoa mitchilli	3.5 (1.65)	0.0 (0.00)	0.0 (0.00)	10.6 (4.25)	1.7 (1.12)	0.1 (0.07)	0.0 (0.00)	5.0 (3.30)
Gobionellus boleosoma	3.3 (0.82)	5.1 (1.86)	4.0 (1.28)	0.9 (0.59)	1.6 (0.32)	2.1 (0.60)	1.8 (0.68)	1.0 (0.29)
Symphurus plagiusa	1.2 (0.35)	1.0 (0.30)	0.4 (0.22)	2.2 (0.94)	1.7 (0.32)	1.5 (0.48)	1.1 (0.59)	2.4 (0.55)
Sciaenops ocellatus	0.7 (0.26)	0.8 (0.55)	0.4 (0.22)	0.8 (0.51)	1.0 (0.57)	2.5 (1.69)	0.2 (0.08)	0.4 (0.17)
Cynoscion nebulosus	0.2 (0.09)	0.3 (0.15)	0.2 (0.20)	0.1 (0.10)	0.5 (0.17)	1.2 (0.47)	0.2 (0.12)	0.2 (0.11)
Mugil cephalus	0.1 (0.09)	0.2 (0.20)	0.2 (0.20)	0.0 (0.00)	0.4 (0.19)	0.4 (0.35)	0.8 (0.46)	0.0 (0.05)
Brevoortia patronus	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.5 (0.45)	1.4 (1.35)	0.0 (0.00)	0.0 (0.00)
Crustaceans	234.5 (48.76)	510.1 (87.76)	167.0 (38.79)	26.3 (3.81)	243.6 (49.05)	523.8 (121.20)	167.1 (32.39)	39.9 (7.21)
Palaemonetes pugio	105.5 (27.28)	253.7 (55.34)	62.3 (16.19)	0.6 (0.34)	136.1 (31.90)	308.0 (80.17)	94.5 (22.53)	5.7 (2.28)
Penaeus setiferus	51.5 (16.86)	79.0 (27.82)	60.0 (41.63)	15.6 (2.37)	30.6 (9.31)	51.6 (25.16)	23.8 (11.11)	16.3 (3.87)
Palaemonetes vulgaris	25.7 (11.19)	76.9 (27.82)	0.1 (0.10)	0.1 (0.10)	18.4 (7.93)	52.8 (22.15)	2.2 (1.43)	0.3 (0.16)
Palaemonetes intermedius	12.0 (5.97)	35.6 (15.85)	0.2 (0.20)	0.2 (0.20)	20.5 (8.09)	55.7 (22.39)	5.6 (3.17)	0.3 (0.25)
Callinectes sapidus	17.1 (2.58)	28.3 (4.00)	19.7 (3.41)	3.3 (0.91)	9.5 (1.58)	16.5 (3.05)	9.2 (2.97)	3.0 (0.49)
Clibanarius vittatus	8.1 (2.65)	8.7 (4.23)	15.2 (6.14)	0.5 (0.34)	10.2 (3.67)	20.9 (10.45)	7.9 (2.49)	1.7 (0.60)
Penaeus aztecus	8.8 (1.86)	17.6 (3.06)	4.6 (1.14)	4.1 (3.14)	3.6 (0.73)	6.8 (1.71)	2.1 (0.87)	2.0 (0.64)
Molluscs	4.6 (1.61)	2.9 (0.92)	8.9 (4.52)	2.1 (0.78)	9.1 (2.11)	5.5 (1.63)	19.2 (5.44)	2.7 (1.03)
Littoraria irrorata	3.4 (1.59)	2.1 (0.95)	8.2 (4.42)	0.0 (0.00)	7.6 (2.10)	4.7 (1.62)	18.3 (5.40)	0.0 (0.00)
Mean size								
Palaemonetes pugio	20.3 (0.77)	20.8 (0.87)	20.5 (1.41)	18.1 (2.94)	14.2 (0.81)	15.8 (1.18)	13.5 (1.04)	12.6 (2.25)
Penaeus setiferus	26.1 (2.25)	23.6 (3.36)	23.9 (4.30)	30.5 (4.03)	27.0 (6.07)	23.4 (2.58)	39.4 (20.66)	20.6 (2.78)
Callinectes sapidus	12.5 (1.16)	14.8 (2.25)	13.0 (1.60)	8.2 (1.00)	12.4 (1.28)	16.6 (2.65)	12.9 (1.90)	7.0 (0.93)
Penaeus aztecus	21.8 (2.03)	20.9 (1.63)	20.6 (2.19)	25.9 (8.92)	21.5 (1.65)	23.0 (2.28)	27.0 (3.77)	14.4 (1.17)
SPRING 1991								
Total macrofauna	262.9 (84.32)	179.3 (30.16)	222.1 (45.12)	387.3 (251.20)	135.7 (22.26)	126.5 (16.85)	173.3 (26.47)	107.2 (59.28)
Fishes	134.4 (86.66)	18.7 (3.28)	14.8 (2.64)	369.7 (251.68)	46.9 (20.13)	27.4 (5.49)	19.9 (5.48)	93.3 (59.48)
Brevoortia patronus	128.3 (93.06)	0.3 (0.21)	0.0 (0.00)	358.9 (252.09)	29.6 (20.23)	5.2 (3.36)	0.4 (0.28)	83.1 (59.69)
Lagodon rhomboides	5.4 (1.31)	8.6 (2.20)	7.0 (2.77)	0.6 (0.27)	3.8 (1.36)	8.3 (3.73)	2.1 (1.11)	0.8 (0.61)
Gobionellus boleosoma	1.9 (0.69)	2.9 (1.76)	1.5 (0.92)	1.3 (0.70)	3.0 (1.23)	4.7 (3.12)	3.6 (1.92)	0.8 (0.39)
Mugil curema	0.6 (0.37)	0.7 (0.70)	1.0 (0.89)	0.0 (0.00)	2.9 (1.49)	1.8 (1.72)	6.8 (4.04)	0.0 (0.00)
Crustaceans	115.8 (20.07)	158.6 (31.67)	171.2 (35.28)	17.6 (5.55)	83.9 (12.68)	98.6 (16.66)	140.6 (26.74)	12.4 (2.87)
Palaemonetes pugio	61.5 (15.60)	76.8 (26.69)	107.5 (30.99)	0.1 (0.10)	49.3 (9.74)	57.7 (16.15)	88.9 (19.87)	1.3 (0.55)
Penaeus aztecus	38.3 (7.50)	61.2 (17.75)	41.0 (8.10)	12.8 (5.64)	9.5 (1.34)	13.0 (1.84)	11.7 (3.08)	3.8 (1.06)
Clibanarius vittatus	5.1 (1.80)	7.3 (3.09)	7.2 (4.29)	0.9 (0.41)	10.2 (5.24)	9.6 (3.09)	19.7 (15.39)	1.3 (0.75)
Callinectes sapidus	6.2 (1.29)	6.8 (1.87)	11.3 (2.41)	0.4 (0.27)	5.4 (0.89)	9.8 (2.01)	5.7 (0.99)	0.7 (0.19)
Penaeus setiferus	0.7 (0.58)	0.4 (0.40)	0.0 (0.00)	1.7 (1.70)	2.8 (0.84)	1.2 (0.86)	3.3 (1.73)	3.8 (1.61)
Molluscs	12.7 (6.38)	2.0 (1.12)	36.1 (17.36)	0.0 (0.00)	4.9 (1.80)	0.5 (0.29)	12.8 (4.93)	1.5 (0.61)
Littoraria irrorata	12.6 (6.39)	1.8 (1.13)	36.1 (17.36)	0.0 (0.00)	4.2 (1.81)	0.0 (0.06)	12.4 (4.96)	0.0 (0.00)
Mean size								
Palaemonetes pugio	26.8 (1.31)	26.5 (1.78)	28.6 (1.50)	12.5	20.2 (1.27)	23.9 (1.61)	19.6 (1.91)	14.3 (2.92)
Penaeus aztecus	40.1 (1.56)	40.2 (2.10)	37.0 (2.61)	43.0 (3.24)	41.2 (1.66)	38.0 (3.23)	42.6 (2.44)	44.1 (2.43)
Callinectes sapidus	26.7 (1.57)	24.4 (2.61)	29.3 (2.08)	25.0 (2.50)	24.0 (2.43)	21.1 (2.53)	27.6 (3.31)	22.5 (10.42)

of fishes (mostly gulf menhaden on subtidal bottom) in natural marshes was 2.9 times higher than in created marshes, but the high variability in the samples prevented the detection of any statistical significance (Table 3). However, densities of *Lagodon rhomboides*, the dominant fish on the marsh surface, were significantly higher (ANOVA contrast p-value < 0.001) in natural compared with created marshes (Table 2). There was no apparent relationship between fish density and the age of created marshes (Fig. 2; all p-values > 0.09 for age/density regressions).

Decapod crustaceans

Decapod crustaceans dominated the fauna in drop samples (91.7% in the fall and 52.6% in the spring). In the fall, 3 species of grass shrimp *Palaemonetes* spp. made up 68.3% of the crustaceans. Juveniles of commercially-important species including white shrimp *Penaeus setiferus*, blue crab *Callinectes sapidus*, and brown shrimp *Penaeus aztecus* were also abundant in the marshes during this season (Table 2). In the spring, the daggerblade grass shrimp *Palaemonetes pugio* was

most abundant (56.3% of crustaceans) along with brown shrimp, thinstripe hermit crab *Clibanarius vittatus*, and blue crab. Most crustaceans were found within vegeta-

tion; 95% were collected in edge or inner marsh samples. The density of crustaceans as a group was not significantly different between natural and created

Table 3. ANOVA results for animals collected in drop samples. The main effect of Marsh and the Marsh × Habitat interaction were partitioned through contrasts comparing natural (Nat) and created (Crt) marshes and the 3 habitats examined [Edge, Inner marsh (Inner), and Nonvegetated bottom (NV)]. Data were ln(y+1)-transformed

Source of variance	df	Fall 1990 SS	p	df	Spring 1991 SS	p	Source of variance	df	Fall 1990 SS	p	df	Spring 1991 SS	p
Fishes							**Penaeus setiferus**						
Marsh	14	33.05	<0.001	13	36.21	0.026	Marsh	14	100.25	<0.001			
Nat vs Crt	1	4.14	0.004	1	1.37	0.303	Nat vs Crt	1	11.82	0.002			
Habitat	2	6.35	0.002	2	3.10	0.302	Habitat	2	10.98	0.010			
Marsh × Habitat	28	34.98	0.001	26	48.34	0.126	Marsh × Habitat	28	94.91	<0.001			
Edge; Nat vs Crt	1	1.24	0.105	1	0.07	0.812	Edge; Nat vs Crt	1	3.45	0.079			
Inner; Nat vs Crt	1	2.79	0.017	1	0.03	0.874	Inner; Nat vs Crt	1	8.45	0.007			
NV; Nat vs Crt	1	0.55	0.278	1	4.47	0.066	NV; Nat vs Crt	1	1.41	0.255			
Crt; Edge vs NV	1	0.10	0.633	1	0.32	0.615	Crt; Edge vs NV	1	0.80	0.392			
Crt; Edge vs Inner	1	3.68	0.007	1	1.28	0.318	Crt; Edge vs Inner	1	9.78	0.004			
Nat; Edge vs NV	1	0.00	0.889	1	2.81	0.142	Nat; Edge vs NV	1	1.45	0.249			
Nat; Edge vs Inner	1	0.76	0.201	1	0.20	0.690	Nat; Edge vs Inner	1	1.69	0.215			
Error	45	20.39		42	52.75		Error	45	48.08				
Crustaceans							**Callinectes sapidus**						
Marsh	14	22.23	<0.001	13	25.83	<0.001	Marsh	14	28.55	<0.001	13	13.87	<0.001
Nat vs Crt	1	0.83	0.161	1	2.64	0.016	Nat vs Crt	1	8.14	<0.001	1	0.07	0.581
Habitat	2	88.86	<0.001	2	94.20	<0.001	Habitat	2	36.49	<0.001	2	47.82	<0.001
Marsh × Habitat	28	57.81	<0.001	26	19.48	0.046	Marsh × Habitat	28	31.59	<0.001	26	14.49	0.003
Edge; Nat vs Crt	1	1.60	0.054	1	1.16	0.105	Edge; Nat vs Crt	1	4.80	<0.001	1	0.36	0.205
Inner; Nat vs Crt	1	0.56	0.247	1	0.73	0.193	Inner; Nat vs Crt	1	7.75	<0.001	1	2.53	0.001
NV; Nat vs Crt	1	0.19	0.498	1	0.78	0.182	NV; Nat vs Crt	1	0.00	0.957	1	0.30	0.244
Crt; Edge vs NV	1	48.28	<0.001	1	40.88	<0.001	Crt; Edge vs NV	1	15.62	<0.001	1	23.98	<0.001
Crt; Edge vs Inner	1	8.02	<0.001	1	0.35	0.366	Crt; Edge vs Inner	1	3.77	0.002	1	1.16	0.025
Nat; Edge vs NV	1	40.81	<0.001	1	24.38	<0.001	Nat; Edge vs NV	1	22.28	<0.001	1	13.01	<0.001
Nat; Edge vs Inner	1	5.99	<0.001	1	0.06	0.704	Nat; Edge vs Inner	1	0.74	0.155	1	1.27	0.019
Error	45	18.44		42	17.64		Error	45	15.93		42	9.02	
Palaemonetes pugio							**Infauna**						
Marsh	14	33.81	0.153	13	26.65	0.288	Marsh	14	36.24	0.003	13	75.43	<0.001
Nat vs Crt	1	0.68	0.519	1	0.09	0.813	Nat vs Crt	1	3.19	0.064	1	2.27	0.122
Habitat	2	259.78	<0.001	2	204.08	<0.001	Habitat	2	0.40	0.800	2	0.50	0.761
Marsh × Habitat	28	87.79	0.023	26	49.66	0.332	Marsh × Habitat	28	42.69	0.051	26	32.60	0.175
Edge; Nat vs Crt	1	2.03	0.268	1	0.79	0.492	Edge; Nat vs Crt	1	1.70	0.174	1	4.79	0.027
Inner; Nat vs Crt	1	0.74	0.503	1	0.52	0.576	Inner; Nat vs Crt	1	0.30	0.565	1	0.21	0.635
NV; Nat vs Crt	1	3.99	0.123	1	1.18	0.403	NV; Nat vs Crt	1	5.47	0.017	1	0.64	0.408
Crt; Edge vs NV	1	131.97	<0.001	1	57.30	<0.001	Crt; Edge vs NV	1	0.06	0.797	1	0.47	0.478
Crt; Edge vs Inner	1	10.20	0.016	1	6.80	0.049	Crt; Edge vs Inner	1	0.18	0.653	1	0.49	0.466
Nat; Edge vs NV	1	122.96	<0.001	1	54.55	<0.001	Nat; Edge vs NV	1	0.53	0.446	1	0.64	0.407
Nat; Edge vs Inner	1	17.96	0.002	1	3.22	0.170	Nat; Edge vs Inner	1	1.69	0.174	1	3.38	0.061
Error	45	72.74		42	69.50		Error	45	39.91		41	37.30	
Penaeus aztecus							**Streblospio benedicti**						
Marsh	14	30.77	<0.001	13	45.64	<0.001	Marsh	14	74.19	<0.001	13	62.42	<0.001
Nat vs Crt	1	10.75	<0.001	1	30.67	<0.001	Nat vs Crt	1	4.72	0.029	1	4.83	0.035
Habitat	2	24.14	<0.001	2	30.02	<0.001	Habitat	2	4.52	0.100	2	2.98	0.244
Marsh × Habitat	28	42.26	<0.001	26	36.74	0.001	Marsh × Habitat	28	81.11	<0.001	26	34.61	0.218
Edge; Nat vs Crt	1	10.52	<0.001	1	11.25	<0.001	Edge; Nat vs Crt	1	0.78	0.366	1	7.01	0.012
Inner; Nat vs Crt	1	5.04	0.001	1	13.54	<0.001	Inner; Nat vs Crt	1	0.66	0.405	1	0.00	0.950
NV; Nat vs Crt	1	0.04	0.768	1	6.54	<0.001	NV; Nat vs Crt	1	13.63	<0.001	1	1.30	0.266
Crt; Edge vs NV	1	6.22	<0.001	1	15.83	<0.001	Crt; Edge vs NV	1	0.69	0.395	1	0.07	0.796
Crt; Edge vs Inner	1	7.38	<0.001	1	2.50	0.028	Crt; Edge vs Inner	1	0.39	0.519	1	0.03	0.875
Nat; Edge vs NV	1	19.43	<0.001	1	13.45	<0.001	Nat; Edge vs NV	1	3.41	0.062	1	2.54	0.122
Nat; Edge vs Inner	1	7.76	<0.001	1	0.79	0.207	Nat; Edge vs Inner	1	3.65	0.054	1	6.42	0.016
Error	45	18.49		42	20.22		Error	45	41.93		42		

marshes in the fall (Tables 2 & 3); but in the spring, the density was significantly higher in natural marshes (115.8 animals per 2.6 m^2 sample) compared with created marshes (83.9 animals per 2.6 m^2 sample). There was no evidence for a relationship between marsh age and overall crustacean density (Fig. 2; regression p-values > 0.20).

All caridean shrimp in the genus *Palaemonetes* (grass shrimp) showed a strong affinity for marsh vegetation, and most were found in edge habitat (Table 2). *P. pugio* was abundant during both seasons, and there were no significant differences in density between natural and created marshes (Table 3). *P. vulgaris* and *P. intermedius* occurred mainly in fall samples and almost exclusively in edge habitat. There was no significant difference in densities of *P. intermedius* between natural and created marshes in fall (ANOVA contrast p-values > 0.12), but *P. vulgaris* was found in significantly greater numbers in natural marshes (ANOVA contrast in edge habitat, p-value < 0.001). Although densities of *P. pugio* were not different among the marshes, the mean size of these shrimp was significantly larger (by 33 to 43%) in natural marshes compared with created marshes (Table 2, ANOVA contrast p-values < 0.003). The size of daggerblade grass shrimp also differed significantly among habitats (ANOVA p-values < 0.028), with the largest mean sizes (fall 17.5 mm TL, spring 25.0 mm) occurring in edge habitat and the smallest on nonvegetated bottom (fall 13.7 mm, spring 14.1 mm). Neither density nor size of *P. pugio* was significantly related to the age of created marshes (regression p-values > 0.26).

Mean densities of the 3 commercially-important crustaceans (*Penaeus aztecus*, *Penaeus setiferus*, *Callinectes sapidus*) were greatest in edge habitat and were significantly higher in natural marshes compared with created marshes (Tables 2 & 3). Densities of *P. aztecus* in natural marshes were 2.4 and 4.0 times higher than in created marshes during fall and spring respectively, while densities of *C. sapidus* were 1.8 and 2.0 times higher in natural marshes during these sampling periods. *P. setiferus* was mainly present in fall samples, and densities were 1.7 times higher in natural marshes than in created marshes. During spring, *P. setiferus* only occurred in 20 of the 84 samples collected. There were no apparent relationships between densities of any of these decapod crustaceans and age of created marshes, and regressions with age were not significant (p-values > 0.08). The mean size of *P. aztecus* and *P. setiferus* did not differ among habitats
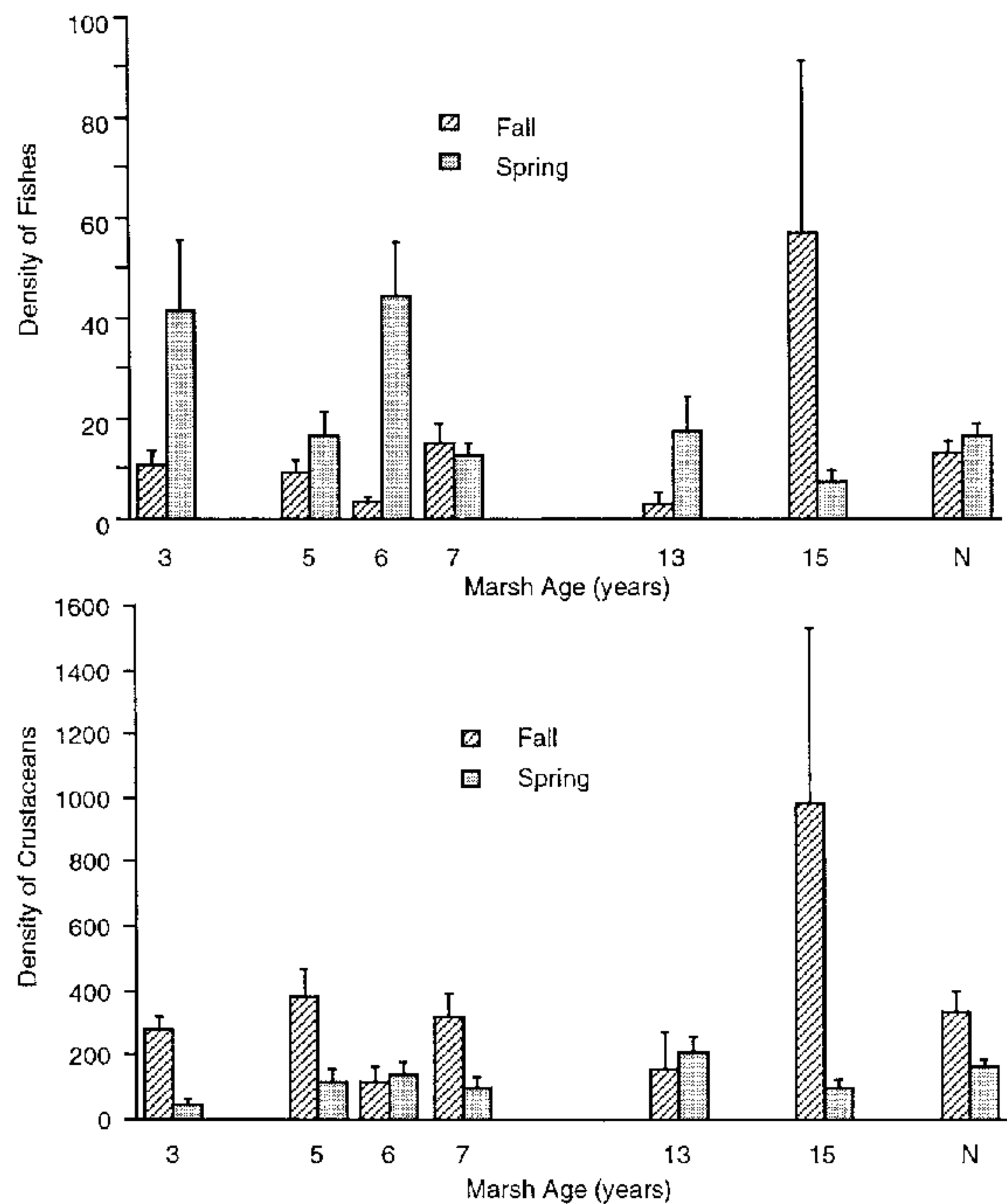

Fig. 2. Densities of fishes and decapod crustaceans at marshes of different ages (yr) and at natural marshes (N). Mean densities per 2.6 m^2 drop sample (error bar represents 1 SE) are shown for all samples collected on the marsh surface (edge and inner marsh habitats). See Table 1 to identify marshes in each age category

or marshes (Table 2, ANOVA p-values > 0.20). The size of *C. sapidus* could only be analyzed in fall (only 25 size observations were available in spring); and although there were differences among marshes (ANOVA p-value = 0.035), blue crab size was not significantly different between natural and created marshes (contrast p-values > 0.65). Crab size varied among habitats (ANOVA p-value = 0.005), and blue crabs on nonvegetated bottom (mean CW = 7.3 mm) were significantly smaller than crabs in both the edge (15.9 mm) and inner marsh (12.9 mm CW) habitat (Scheffe's multiple comparison test, alpha = 0.05).

The thinstripe hermit crab *Clibanarius vittatus* was present on the marsh surface during both fall and spring (Table 2). During both seasons, mean densities of this species were greater in the created marshes compared with natural marshes, but these differences were not statistically significant (ANOVA contrast p-values > 0.06). Densities of thinstripe hermit crabs were significantly related to the age of created marshes in fall (regression p-value < 0.001). This rela-

tionship was negative with highest densities in the youngest marshes; marsh age could explain 28% of the variability in density of the species.

Molluscs

The marsh periwinkle *Littoraria irrorata* comprised 82% of molluscs in fall and 93% in spring (Table 2). Almost all (94%) marsh periwinkles were collected within vegetated habitat, and mean densities were highest in inner marsh samples. In ANOVAs there were significant differences among marshes (p-values < 0.02) during both seasons, but only in the spring was there a difference between created and natural marshes (contrast p-value = 0.025); densities in natural marshes were 3 times higher than those in created marshes. This difference appeared to be mainly due to densities in the edge habitat.

Sediment cores

There was little seasonal variability in macro-organic matter (Table 4), and mean dry weight (both seasons combined) was significantly higher (ANOVA contrast p-values all < 0.006) in natural marshes (6.3 g core^{-1}, n = 57, SE = 0.65) compared with created marshes (2.2 g core^{-1}, n = 112, SE = 0.35). The amount of MOM in sediments also varied among habitats, and values were significantly higher within vegetation than on nonvegetated bottom (Table 4, ANOVA contrast p-values < 0.001).

Infauna were dominated by annelid worms (88.8 and 93.5% of the total organisms in the fall and spring, respectively); the most abundant was the polychaete *Streblospio benedicti*. Densities of overall infauna and *S. benedicti* were not significantly different among the 3 habitats examined during either season (Table 3). In fall, mean densities of both total infauna and *S. bene-dicti* in all habitats were higher in natural marshes than in created marshes, but the difference was only significant on nonvegetated bottom (Tables 3 & 4). In spring, mean densities of total infauna in natural and created marshes were generally similar; but in the edge habitat there was a significant difference (Table 3), and the log-transformed density was higher in natural marshes. Spring densities of *S. benedicti* in all habitats were significantly higher in natural marshes than in created marshes (Table 3). Fall densities of another abundant polychaete, *Capitella capi-tata*, were significantly higher in natural marshes than in created marshes (inner marsh, ANOVA contrast p-value = 0.026); this comparison was not significant in spring. Densities of peracarid crustaceans (mainly

amphipods and the tanaid *Hargeria rapax*) were also significantly higher in natural marshes than in created marshes (ANOVA contrast p-values < 0.001); natural marsh densities were 8.4 times higher in fall and 1.3 times higher in spring (Table 4).

MOM was positively related to the age of created marshes (regression p-value = 0.009, n = 74), although the relationship only explained 9% of the variability in MOM. There were no apparent positive relationships between marsh age and infaunal density; regressions between the age of created marshes and densities of total infauna, annelid worms, *Streblospio benedicti* (spring only), *Capitella capitata*, and peracarid crustaceans were not statistically significant (all regression p-values > 0.10). Fall densities of *S. benedicti* on the marsh surface were highest in the youngest marshes, and there was a significant negative regression (p-value = 0.01) with marsh age that could explain 16% of the variability within created marshes.

Species richness

Species richness in marshes was examined by counting the total number of species (within fishes, decapod crustaceans, and infauna) collected in the 6 samples (15.6 m^2 of area for nekton and 471 cm^2 for infauna) from each marsh. The mean number of fish species from all marshes was 9.9 in the fall and 12.8 in the spring, while the mean number of decapod species was 12.2 in fall and 7.8 in spring. There were no significant differences in species richness for these groups between natural and created marshes (1-way ANOVA, p-values > 0.48). Species richness within the infauna, however, appeared greater in natural marshes than in created marshes. The mean number of infaunal species identified in fall was 14.2 in natural marshes and 11.2 in created marshes, but this difference was not statistically significant (ANOVA p-values = 0.22). The difference between natural (15.2 species) and created (10.2 species) marshes in spring, however, was statistically significant (ANOVA p-value = 0.032).

Physical and chemical parameters

Statistically significant differences were generally found among habitats and marshes (including the contrasts between created and natural marshes) for the physical and chemical parameters measured, but differences in temperature, salinity, and dissolved oxygen did not appear to be biologically meaningful. In fall, mean values among the 3 habitats ranged from 25.2 to 26.1°C for temperature, 19.8 to 20.2 ppt for salinity, and 5.6 to 7.0 ppm for dissolved oxygen. In spring, these

Table 4. Mean densities and (in parentheses) standard errors of common infaunal organisms (≥30 individuals collected) and sediment macro-organic matter collected from 78.5 cm² sediment cores taken within each drop sample. Each habitat mean in natural marshes is from 10 cores; habitat means in created marshes are from 18 (spring) or 20 (fall) cores. All marsh cores (Edge and Inner marsh) were taken between clumps of vegetation

	Natural marshes				Created marshes			
	All habitats	Edge	Inner	Nonveg	All habitats	Edge	Inner	Nonveg
FALL 1990								
Macro-organic matter (g dry wt)	6.1 (0.84)	8.0 (1.44)	7.4 (1.18)	2.6 (1.10)	2.4 (0.57)	2.1 (0.45)	4.7 (1.53)	0.4 (0.26)
Total infauna	46.0 (10.29)	52.9 (22.75)	37.9 (20.01)	47.1 (9.63)	28.6 (4.81)	33.9 (10.95)	31.9 (7.95)	20.0 (5.14)
Annelids	37.4 (7.85)	36.8 (14.70)	32.6 (17.03)	42.8 (9.16)	27.1 (4.69)	32.5 (10.75)	29.6 (7.59)	19.1 (5.16)
Polychaetes	34.8 (7.82)	32.9 (13.83)	28.8 (17.42)	42.7 (9.18)	23.1 (4.42)	27.0 (10.00)	24.2 (7.22)	18.1 (5.21)
Streblospio benedicti	23.0 (7.03)	22.7 (10.89)	19.3 (16.36)	26.9 (9.41)	12.6 (3.81)	16.2 (8.87)	12.0 (5.58)	9.7 (4.94)
Capitella capitata	3.9 (0.70)	2.8 (1.03)	4.6 (1.09)	4.3 (1.51)	3.3 (0.67)	3.5 (1.09)	4.0 (1.62)	2.3 (0.56)
Parandalia ocularis	2.0 (1.07)	1.1 (0.82)	0.0 (0.00)	5.0 (2.98)	1.9 (0.58)	1.2 (0.71)	2.9 (1.45)	1.5 (0.66)
Nereidae. unidentified	1.0 (0.42)	1.3 (0.84)	1.0 (0.70)	0.8 (0.70)	1.0 (0.40)	1.9 (1.03)	0.0 (0.05)	1.1 (0.59)
Hobsonia gunneri	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	0.0 (0.00)	1.5 (1.45)	0.0 (0.00)	4.4 (4.35)	0.0 (0.00)
Mediomastus californiensis	0.8 (0.49)	0.8 (0.80)	0.0 (0.00)	1.7 (1.25)	0.9 (0.30)	1.5 (0.79)	0.2 (0.16)	1.1 (0.39)
Nereis (Neanthes) succinea	1.9 (0.75)	2.3 (1.01)	2.3 (1.71)	1.2 (1.20)	0.3 (0.12)	0.4 (0.26)	0.3 (0.25)	0.0 (0.05)
Heteromastus filiformis	0.5 (0.24)	0.3 (0.21)	0.1 (0.10)	1.2 (0.65)	0.8 (0.25)	0.8 (0.55)	0.2 (0.11)	1.3 (0.49)
Oligochaetes	2.6 (1.23)	3.9 (3.25)	3.8 (1.70)	0.1 (0.10)	4.0 (1.97)	5.6 (4.98)	5.4 (3.23)	1.1 (0.47)
Crustaceans	7.1 (3.13)	12.3 (8.75)	5.2 (3.39)	3.9 (1.43)	0.9 (0.21)	0.8 (0.38)	1.2 (0.47)	0.6 (0.20)
Amphipods	2.0 (0.78)	2.9 (2.00)	0.9 (0.53)	2.3 (1.15)	0.3 (0.12)	0.4 (0.30)	0.3 (0.16)	0.2 (0.11)
Corophium spp.	0.9 (0.46)	1.4 (0.95)	0.4 (0.27)	1.0 (1.00)	0.0 (0.05)	0.1 (0.10)	0.0 (0.00)	0.1 (0.10)
Other crustaceans								
Hargeria rapax	4.3 (2.29)	8.8 (6.31)	3.8 (2.60)	0.4 (0.31)	0.2 (0.15)	0.0 (0.00)	0.6 (0.46)	0.0 (0.05)
Calanoid copepod	1.0 (0.69)	2.8 (2.00)	0.0 (0.00)	0.1 (0.10)	0.2 (0.12)	0.1 (0.07)	0.4 (0.35)	0.0 (0.00)
SPRING 1991								
Macro-organic matter (g dry wt)	6.4 (0.98)	8.6 (1.79)	7.6 (2.02)	3.4 (0.81)	2.1 (0.39)	2.5 (0.67)	3.7 (0.78)	0.2 (0.06)
Total infauna	31.2 (4.19)	40.7 (8.32)	22.9 (6.44)	30.9 (6.68)	35.4 (6.07)	43.3 (15.44)	29.0 (6.56)	34.1 (7.54)
Annelids	28.5 (3.85)	38.1 (7.68)	19.1 (5.25)	29.2 (6.33)	33.5 (5.50)	39.8 (13.78)	27.3 (5.86)	33.4 (7.38)
Polychaetes	25.9 (3.78)	35.3 (7.28)	16.4 (5.45)	26.9 (6.15)	31.6 (5.28)	38.0 (13.07)	23.7 (5.31)	33.2 (7.44)
Streblospio benedicti	12.9 (2.53)	18.1 (4.98)	8.4 (3.48)	12.6 (4.57)	10.2 (3.56)	17.1 (10.04)	7.3 (3.13)	6.3 (1.99)
Tharyx marione	0.0 (0.05)	0.0 (0.00)	0.1 (0.10)	0.1 (0.10)	8.0 (2.43)	5.0 (3.06)	4.7 (2.61)	14.2 (5.97)
Capitella capitata	3.9 (1.07)	4.4 (1.98)	3.8 (1.87)	3.5 (1.92)	5.0 (1.41)	7.0 (3.09)	5.6 (2.79)	2.4 (0.75)
Mediomastus californiensis	1.7 (0.65)	1.3 (0.60)	0.3 (0.30)	3.3 (1.70)	2.8 (0.69)	1.9 (1.07)	1.1 (0.61)	5.3 (1.54)
Nereidae. unidentified	2.4 (0.94)	4.9 (2.81)	1.9 (0.71)	0.8 (0.51)	1.2 (0.44)	1.1 (0.71)	0.8 (0.57)	1.7 (0.99)
Polydora ligni	0.8 (0.35)	0.7 (0.37)	1.3 (0.91)	0.5 (0.34)	1.7 (0.95)	2.9 (2.43)	2.0 (1.50)	0.0 (0.06)
Nereis (Neanthes) succinea	2.2 (1.00)	3.8 (2.43)	0.2 (0.13)	2.7 (1.89)	0.7 (0.33)	1.1 (0.90)	1.0 (0.39)	0.0 (0.00)
Heteromastus filiformis	0.7 (0.33)	0.7 (0.47)	0.0 (0.00)	1.4 (0.83)	1.5 (0.43)	1.4 (0.73)	0.7 (0.39)	2.2 (1.01)
Parandalia ocularis	0.6 (0.39)	0.2 (0.15)	0.0 (0.00)	1.6 (1.09)	0.3 (0.09)	0.2 (0.12)	0.3 (0.11)	0.4 (0.23)
Oligochaetes	2.6 (1.00)	2.8 (1.71)	2.7 (1.20)	2.3 (2.30)	1.9 (0.66)	1.8 (0.97)	3.6 (1.65)	0.2 (0.22)
Crustaceans	2.0 (0.43)	2.3 (0.93)	2.4 (0.82)	1.4 (0.48)	1.6 (0.65)	3.0 (1.64)	1.5 (0.99)	0.3 (0.18)
Amphipods	1.4 (0.36)	1.8 (0.95)	1.2 (0.47)	1.2 (0.44)	0.5 (0.23)	0.3 (0.18)	1.1 (0.66)	0.1 (0.08)
Gammarus mucronatus	0.7 (0.29)	1.0 (0.76)	1.0 (0.49)	0.0 (0.00)	0.2 (0.08)	0.2 (0.17)	0.4 (0.16)	0.0 (0.00)
Other crustaceans								
Hargeria rapax	0.4 (0.16)	0.4 (0.18)	0.8 (0.42)	0.0 (0.00)	1.0 (0.54)	2.6 (1.56)	0.4 (0.33)	0.1 (0.11)

ranges were 27.2 to 28.1°C, 9.3 to 9.8 ppt, and 7.2 to 7.7 ppm. Mean values for natural/created marshes (all contrast p-values < 0.025 except temperature in spring, p-value = 0.45) were 26.3/25.2°C, 19.8/20.1 ppt, and 7.0/6.1 ppm (DO) in fall and 27.8/27.7°C, 10.3/9.2 ppt, and 7.1/7.7 ppm in spring. These small differences are unlikely to be biologically important for estuarine organisms. Differences in turbidity between natural and created marshes, however, were large and perhaps related to the substratum of dredged material in many created marshes. In fall, the mean turbidity in natural marshes was 17.2 FTU (n = 30, SE = 2.13) compared with 50.3 FTU (n = 60, SE = 8.32) in created marshes. In spring, the values were 5.9 FTU (n = 30, SE = 0.58) in natural marshes and 15.5 FTU (n = 54, SE = 2.76) in created marshes. The contrasts in the ANOVAs for these comparisons were highly significant (p-values < 0.001).

The extent of tidal flooding determines availability of the marsh surface for estuarine nekton. Over the 1 yr period from September 1, 1990 to August 31, 1991, the flooding duration of the marsh edge habitat for the 5 natural marshes ranged between 74 and 80% (Fig. 3). Flooding of the edge habitat in created marshes was more variable (between 43 and 91%), reflecting the substantial variability in elevation of these marshes.
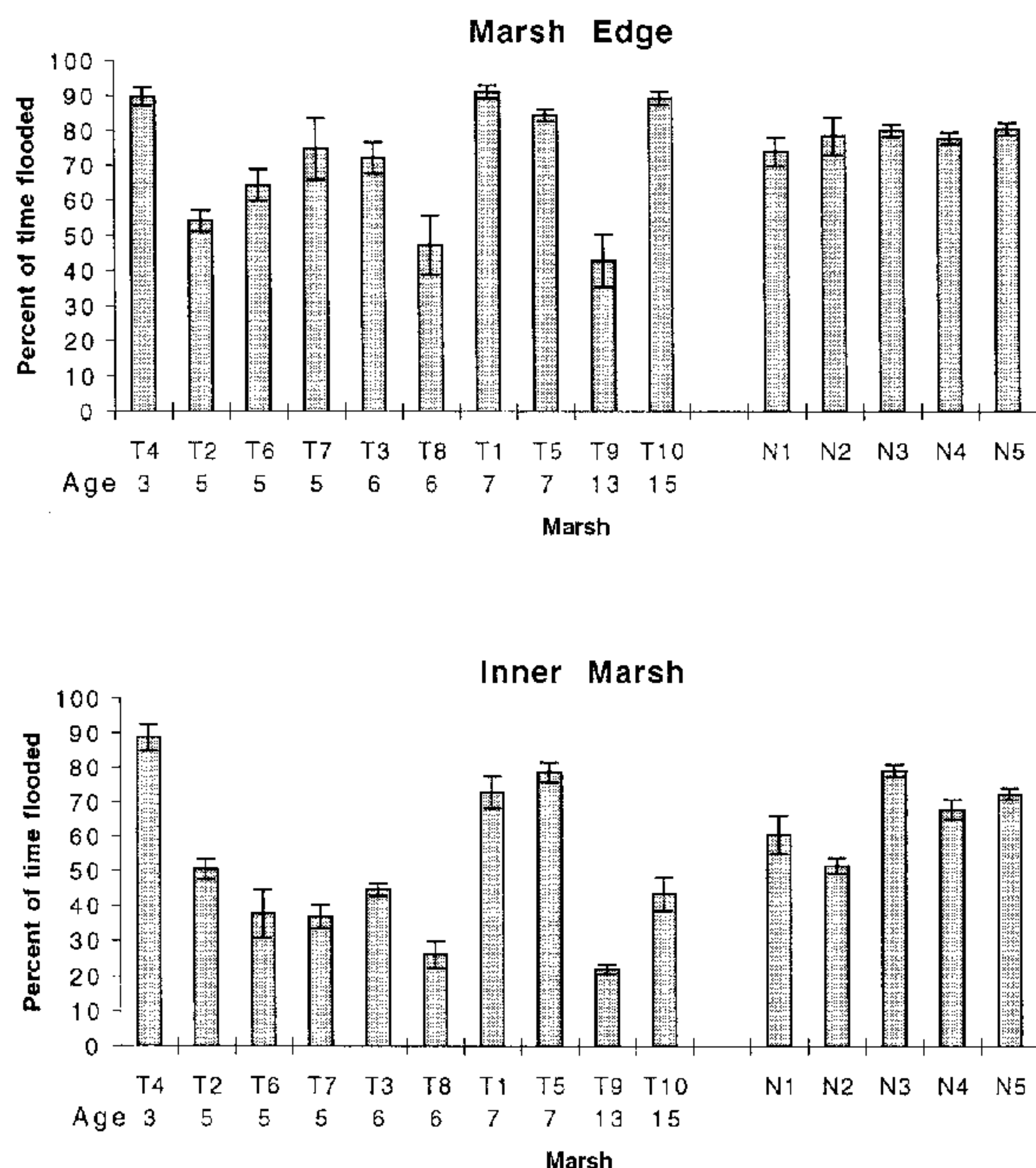
Marsh Edge

Inner Marsh

Fig. 3. Duration of tidal inundation during 1 yr (September 1, 1990 through August 31, 1991). Created marshes (T1 to T10) are arranged in order of their age in years at the time of sampling. The mean percentage of time that each marsh habitat was flooded was determined from 3 water level gauges in the bay system. The standard error bars shown represent variability in the elevation of the marsh surface and in the water level differences between the marsh and the nearest gauge

The overall mean flooding duration was 78.1 % (n = 5, SE = 1.16) for natural marshes and 71.0 % (n = 10, SE = 5.74) for created marshes. Annual flooding of inner marsh habitats was lower and even more variable due to differences in marsh slopes (Fig. 3). The overall mean flooding duration for the inner marsh was 66.3 % (n = 5, SE = 4.77) for natural marshes and 50.1 % (n = 10, SE = 7.14) for created marshes. There was a seasonal pattern to marsh flooding, and mean flooding durations were highest during the spring and fall (Fig. 4). Edge habitat in natural marshes during April and May was flooded between 96 and 99 % of the time, while the inner marsh during these periods was flooded between 88 and 96 % of the time. Even during seasonal low-water periods such as in July and August, the natural marshes were flooded between 44 and 65 % of the time. The lowest monthly mean flooding duration (27 %) occurred during July in the inner marsh habitat of created marshes. As in the annual flooding data, created marshes exhibited much higher

variability in monthly flooding durations than the natural marshes.

Relationships between nekton densities and environmental variables

Multiple regression models used to explore relationships between nekton densities on the marsh surface and environmental factors indicated that the strongest and most consistent relationships were with annual tidal flooding and sample water depth (Table 5). The most important variable for fishes appeared to be water depth, with higher densities of fishes in deeper water. For some fish species, salinity, water temperature, and dissolved oxygen could explain significant portions of the variability in density. Densities of decapod crustaceans were mainly related to our tidal flooding variable, with higher densities in marsh areas that were flooded for extensive periods throughout the year. This relationship was more apparent in fall samples. There is an obvious relationship between water depth and tidal flooding, and the variables were positively correlated (r = 0.74 in fall and 0.93 in spring, p-values < 0.001). Therefore, any relationship between animal densities and either of these variables could be caused by a relationship with the other variable. However, water depth and tidal flooding are not necessarily interdependent because they function on different time scales as an expression of elevation. We included both variables in the model because of their potential for measuring very different relationships. For example, densities of *Clibanarius vittatus* in fall and all decapods in spring were positively related to flooding but negatively related to water depth, suggesting that some crustaceans may select for both shallow water and low elevation habitats that are flooded most of the year. Densities of *Penaeus aztecus* during both seasons and *P. setiferus* in fall were strongly related (negatively) to water turbidity in the analyses; but both low densities of these animals and high turbidities occurred in created marshes, and this density/turbidity relationship may have been caused by some other difference between natural and created marshes. Other variables such as water temperature and salinity were periodically important in the models for some species of crustaceans. The amount of macro-organic matter and the abundance of infauna in sediment cores seldom explained much variability in densities of either fishes

or decapods. Densities of the dominant mollusc, *Littoraria irrorata*, were not significantly related to any of the variables included in the regression models.

Marsh elevation and flooding duration were variable in created marshes and appeared important in explaining densities of nekton. To test whether these variables could explain the overall differences between natural and created marshes, we compared mean densities of fishes and dominant crustaceans among natural marshes, low-elevation created marshes (T1, T3, T4, T5, T7 & T10), and high-elevation created marshes (T2, T6, T8 & T9). Created marshes were assigned to these elevation categories on the basis of marsh edge flooding durations shown in Fig. 3. Only data from the vegetated habitats (edge and inner marsh) were included in this analysis, and we compared marsh categories using contrasts from within the Marsh effect of a 1-way ANOVA. In general, low-elevation marshes were more similar to natural marshes than high-elevation marshes (Table 6). However, significant differences persisted between natural and low-elevation created marshes for densities of *Penaeus aztecus* and *Callinectes sapidus* in both the fall and the spring.
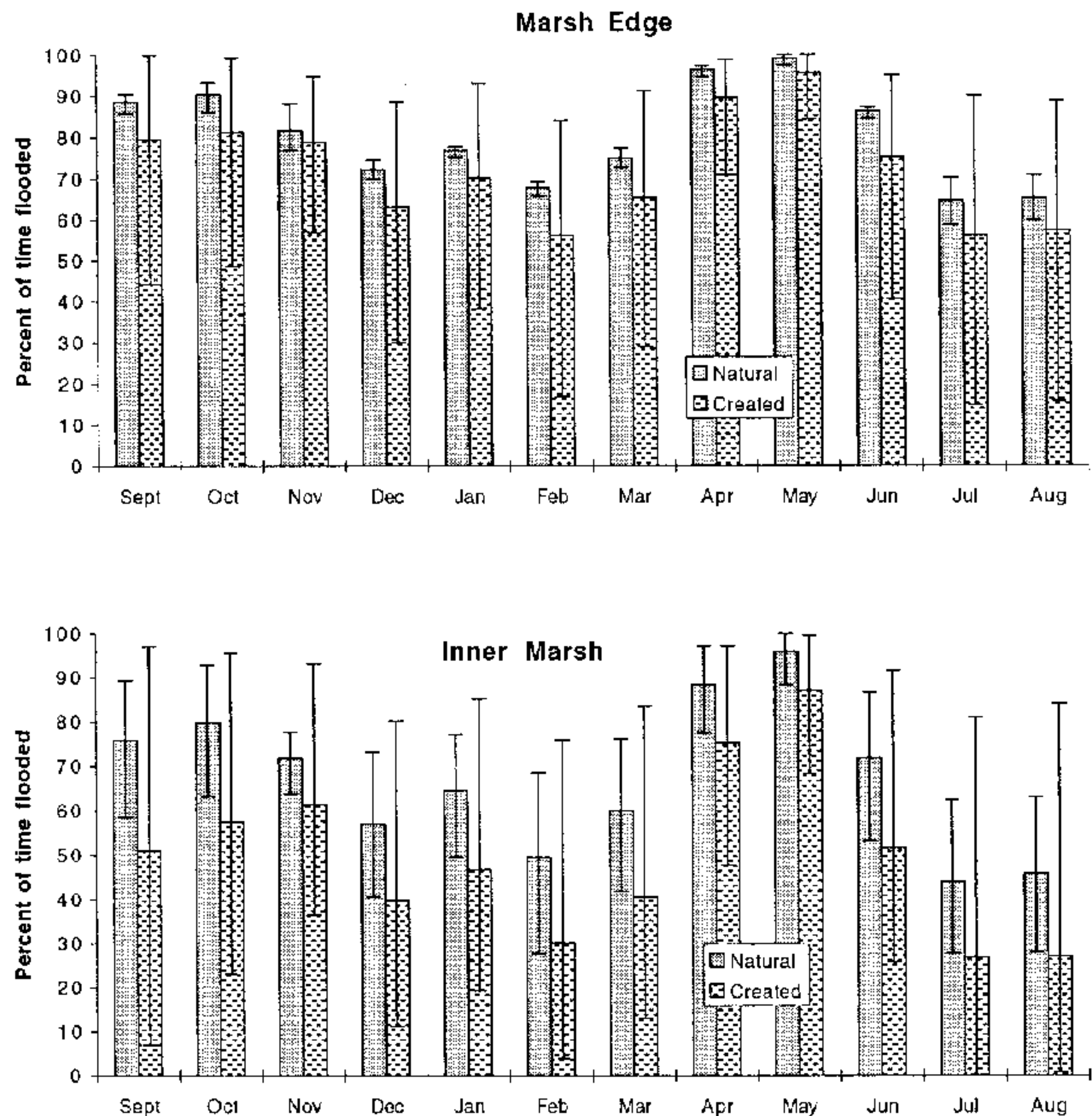

Fig. 4. Duration of tidal inundation at natural and created salt marshes each month from September 1990 through August 1991. Mean flooding percentages are shown; vertical lines through bars represent the range among the 5 natural marshes and the 10 created marshes

DISCUSSION

The function and value of salt marshes for juvenile fishery species and other nekton is difficult to measure. Salt marsh habitats in the northern Gulf of Mexico are directly exploited by many nekton species (Zimmerman & Minello 1984, Thomas et al. 1990, Baltz et al. 1993, Rozas & Reed 1993, Peterson & Turner 1994); and for some species, such as brown shrimp and blue crabs, salt marshes have been shown to function by increasing growth and reducing mortality in comparison with nonvegetated bay bottom (Minello et al. 1989, Thomas 1989, Minello & Zimmerman 1991, Heck & Coen 1995). However, there is evidence that salt marsh functions vary for different nekton species and vary within estuaries and coastal regions (Zimmerman et al. 1990, Minello & Zimmerman 1991, Rozas 1993, Kneib & Wagner 1994, McIvor & Rozas 1996). Such variability should also be expected in the relative value of created marshes in relation to natural marshes. For example, the rate of sediment development in created marshes (based on organic content and benthic infaunal organisms), may be more rapid in Texas (Lindau & Hossner 1981, Minello & Zimmerman 1992) than on the Southeast Coast of the United States (Cammen 1975, Craft et al. 1988, Sacco 1989, Craft et al. 1991, LaSalle et al. 1991, Sacco et al. 1994).

Our study is based primarily on a comparison of animal densities among 5 natural and 10 created salt marshes. This use of animal densities is predicated on the assumption that density distributions reflect a habitat's value in providing essential functions for a species. Although we believe this paradigm is generally accepted (Rozas & Minello 1997), it may not always be true. Measurements of animal growth and mortality within marshes would provide more direct information on relative habitat value, but these measurements are difficult to obtain. Even obtaining density data for nekton within marshes has been a problem (Kushlan 1974, Zimmerman et al. 1984, Kneib 1991, Rozas 1992, Rozas & Minello 1997). We used an enclosure sampler to measure nekton densities on the marsh surface and in adjacent subtidal habitats. Similar quantitative sampling techniques seldom have been used to assess utilization of created marshes (Minello & Zimmerman 1992, Meyer et al. 1993, Streever & Crisman 1993, Minello et al. 1994).

Table 5. Stepwise multiple regression analyses on log-transformed densities of abundant fauna collected in drop samples using 8 independent variables; percent of time flooded over the year (FLOOD), sediment macro-organic matter (MOM), log-transformed abundance of sediment infauna (INF), sample water depth (DEPTH), salinity (SAL), water temperature (TEMP), dissolved oxygen (DO), and turbidity (TURB). The independent variable name is shown in italics if the relationship is negative. Data for each season are from all samples on the marsh surface (n = 57 in fall and 47 in spring). At each step of the analysis, the included variables are shown in order of their partial F-ratio in that model along with the adjusted R^2 value for the model; ns indicates that none of the variables contributed significantly to a model

Dependent variable	Independent variables					
	Step 1	R^2	Step 2	R^2	Final	R^2
FALL						
Total macrofauna	FLOOD	0.43	FLOOD MOM	0.47	FLOOD MOM DEPTH	0.51
Fishes	DEPTH	0.38	DEPTH SAL	0.43	DEPTH SAL	0.43
Gobiosoma bosc	DEPTH	0.26	DEPTH SAL	0.42	DEPTH SAL MOM	0.47
Gobionellus boleosoma	DO	0.23	DO FLOOD	0.27	DO FLOOD	0.27
Symphurus plagiusa	DEPTH	0.29	DEPTH TEMP	0.34	DEPTH TEMP	0.34
Sciaenops occellatus	DEPTH	0.18	DEPTH SAL	0.28	DEPTH SAL	0.28
Cynoscion nebulosus	DEPTH	0.38				
Decapod crustaceans	FLOOD	0.44	FLOOD MOM	0.49	FLOOD MOM DEPTH	0.52
Palaemonetes pugio	FLOOD	0.32				
Penaeus setiferus	TURB	0.28	*TURB DEPTH*	0.38	*TURB DEPTH INF*	0.42
Palaemonetes vulgaris	FLOOD	0.22	FLOOD SAL	0.37	FLOOD SAL	0.37
Palaemonetes intermedius	SAL	0.26	*SAL FLOOD*	0.39	*SAL FLOOD*	0.39
Callinectes sapidus	FLOOD	0.42	FLOOD TURB	0.46	FLOOD TURB	0.46
Clibanarius vittatus	FLOOD	0.14	FLOOD DEPTH	0.24	FLOOD DEPTH TEMP	0.36
Penaeus aztecus	TURB	0.38	*TURB DEPTH*	0.46	*TURB DEPTH MOM DO INF*	0.60
Molluscs						
Littoraria irrorata	ns				ns	
SPRING						
Total macrofauna	*SAL*	0.18	*SAL DEPTH*	0.25	*DEPTH FLOOD*	0.35
Fishes	ns	ns				
Brevoortia patronus	DEPTH	0.19	DEPTH SAL	0.25	DEPTH SAL	0.25
Lagodon rhomboides	DO	0.55	*DO TURB*	0.60	*DO INF SAL TURB*	0.71
Decapod crustaceans	*DEPTH*	0.14	*DEPTH FLOOD*	0.33	*DEPTH FLOOD TURB*	0.39
Palaemonetes pugio	ns	ns				
Penaeus aztecus	FLOOD	0.27	FLOOD TURB	0.37	FLOOD TURB DEPTH	0.47
Callinectes sapidus	*DEPTH*	0.33	*DEPTH*	0.33		
Clibanarius vittatus	DO	0.26			DO	0.26
Molluscs						
Littoraria irrorata	ns				ns	

In general, densities of both fishes and decapod crustaceans were lower in created marshes than in natural marshes. Statistically significant differences were observed for fishes (mainly gobies and pinfish), marsh grass shrimp, brown shrimp, white shrimp, and blue crabs. Densities of commercially important decapods in created marshes were only 25 to 41% of the densities in natural marshes. Nekton densities were never significantly greater in created marshes than in natural marshes. These density results are similar to those observed by Minello & Zimmerman (1992) for other natural and created (2 to 5 yr of age) marshes on the Texas coast. The most abundant decapod crustacean, *Palaemonetes pugio*, the daggerblade grass shrimp, was found in similar numbers in natural and created marshes; but shrimp in created marshes were signifi-

cantly smaller than those in natural marshes. We did not routinely record sex or stage of maturation in our analyses, but a re-examination of several samples suggested that the percentage of *P. pugio* that were gravid females was also lower in the created marshes.

The size and density differences observed for nekton may be due to inadequate food resources in created marshes (Moy & Levin 1991, Shreffler et al. 1992). Macro-organic matter and populations of infaunal organisms in marsh sediments provide food for these fishes and decapods (Morgan 1980, Weisberg et al. 1981, Weisberg & Lotrich 1982, Kneib 1985, 1986, Hunter & Feller 1987, Thomas 1989, Rozas & LaSalle 1990, Feller 1991, McTigue & Zimmerman 1991, Minello & Zimmerman 1991, McTigue 1993, Currin et al. 1995), and both MOM and infaunal densities

ERRATUM

Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA

Thomas J. Minello, James W. Webb, Jr

Mar Ecol Prog Ser 151: 165–179, 1997

• Table 5 on page 176 contained incorrect italicisation and misplaced entries. The corrected table appears below

Table 5. Stepwise multiple regression analyses on log-transformed densities of abundant fauna collected in drop samples using 8 independent variables; percent of time flooded over the year (FLOOD), sediment macro-organic matter (MOM), log-transformed abundance of sediment infauna (INF), sample water depth (DEPTH), salinity (SAL), water temperature (TEMP), dissolved oxygen (DO), and turbidity (TURB). The independent variable name is shown in italics if the relationship is negative. Data for each season are from all samples on the marsh surface (n = 57 in fall and 47 in spring). At each step of the analysis, the included variables are shown in order of their partial F-ratio in that model along with the adjusted R^2 value for the model; ns indicates that none of the variables contributed significantly to a model

| Dependent variable | Independent variables | | | | | |
	Step 1	R^2	Step 2	R^2	Final	R^2
FALL						
Total macrofauna	FLOOD	0.43	FLOOD MOM	0.47	FLOOD MOM DEPTH	0.51
Fishes	DEPTH	0.38	DEPTH *SAL*	0.43	DEPTH *SAL*	0.43
Gobiosoma bosc	DEPTH	0.26	DEPTH *SAL*	0.42	DEPTH *SAL* MOM	0.47
Gobionellus boleosoma	DO	0.23	DO FLOOD	0.27	DO FLOOD	0.27
Symphurus plagiusa	DEPTH	0.29	DEPTH TEMP	0.34	DEPTH TEMP	0.34
Sciaenops occellatus	DEPTH	0.18	DEPTH *SAL*	0.28	DEPTH *SAL*	0.28
Cynoscion nebulosus	DEPTH	0.38				
Decapod crustaceans	FLOOD	0.44	FLOOD MOM	0.49	FLOOD MOM DEPTH	0.52
Palaemonetes pugio	FLOOD	0.32				
Penaeus setiferus	*TURB*	0.28	*TURB* DEPTH	0.38	*TURB* DEPTH *INF*	0.42
Palaemonetes vulgaris	FLOOD	0.22	FLOOD *SAL*	0.37	FLOOD *SAL*	0.37
Palaemonetes intermedius	SAL	0.26	*SAL* FLOOD	0.39	*SAL* FLOOD	0.39
Callinectes sapidus	FLOOD	0.42	FLOOD *TURB*	0.46	FLOOD *TURB*	0.46
Clibanarius vittatus	FLOOD	0.14	FLOOD *DEPTH*	0.24	FLOOD *DEPTH* TEMP	0.36
Penaeus aztecus	*TURB*	0.38	*TURB* DEPTH	0.46	*TURB* DEPTH MOM DO INF	0.60
Molluscs						
Littoraria irrorata	ns				ns	
SPRING						
Total macrofauna	*SAL*	0.18	*SAL DEPTH*	0.25	*DEPTH* FLOOD	0.35
Fishes	ns				ns	
Brevoortia patronus	DEPTH	0.19	DEPTH *SAL*	0.25	DEPTH *SAL*	0.25
Lagodon rhomboides	*DO*	0.55	*DO TURB*	0.60	*DO* INF SAL *TURB*	0.71
Decapod crustaceans	*DEPTH*	0.14	*DEPTH* FLOOD	0.33	*DEPTH* FLOOD *TURB*	0.39
Palaemonetes pugio	ns				ns	
Penaeus aztecus	FLOOD	0.27	FLOOD *TURB*	0.37	FLOOD *TURB DEPTH*	0.47
Callinectes sapidus	*DEPTH*	0.33			*DEPTH*	0.33
Clibanarius vittatus	DO	0.26			DO	0.26
Molluscs						
Littoraria irrorata	ns				ns	

Table 6. Mean densities (no. per 2.6 m² drop sample) and standard errors of fishes and dominant crustaceans for natural marshes, low-elevation created marshes (T1, T3, T4, T5, T7, T10), and high-elevation created marshes (T2, T6, T8, T9). Only data from vegetated habitats (edge and inner marsh) were used in this analysis. Probability values are from contrasts in a 1-way ANOVA on ln-transformed densities

Taxa	Natural Mean (SE)	Low created Mean (SE)	High created Mean (SE)	ANOVA contrast p-values	
				Nat vs Low	Nat vs High
Fall					
Fishes	13.4 (2.00)	18.8 (6.37)	5.8 (1.71)	0.555	0.002
Crustaceans	338.6 (61.07)	409.9 (102.36)	248.8 (71.29)	0.969	0.022
Palaemonetes pugio	158.0 (35.63)	237.7 (65.78)	146.6 (50.94)	0.492	0.164
Penaeus aztecus	11.1 (2.18)	5.8 (1.22)	2.4 (1.69)	0.025	0.000
Penaeus setiferus	69.5 (24.46)	54.2 (22.15)	12.9 (5.76)	0.259	0.000
Callinectes sapidus	24.0 (2.74)	15.5 (3.03)	8.7 (2.82)	0.007	0.000
Spring					
Fishes	16.8 (2.10)	19.0 (4.38)	29.4 (6.66)	0.409	0.257
Crustaceans	164.9 (23.12)	103.2 (19.32)	140.1 (26.27)	0.032	0.435
Palaemonetes pugio	92.2 (20.21)	69.9 (17.57)	77.5 (19.50)	0.318	0.881
Penaeus aztecus	51.1 (9.78)	16.3 (2.35)	7.4 (2.19)	0.002	0.000
Callinectes sapidus	9.0 (1.57)	6.0 (1.77)	9.9 (1.21)	0.007	0.304

(mainly the polychaete worm *Streblospio benedicti*) were significantly lower in our created salt marshes. There was little evidence for strong correlative relationships between these sediment parameters and densities of nekton on the marsh surface, but relationships between prey populations and predator abundance in marshes are complex (Kneib & Stiven 1982, Kneib 1988, Minello & Zimmerman 1992). Information currently being analyzed on benthic microalgae, meiofauna, sediment organic content, and infaunal productivity in these marshes may provide additional insights into nekton distribution patterns.

Perhaps the most defining characteristic of any wetland is its hydrology (Mitsch & Gosselink 1986), and the hydrology of these shoreline *Spartina alterniflora* marshes is mainly determined by tidal flooding patterns. Tidal flooding of the 5 natural marshes was similar; elevations were consistently low and flooding durations were high. In contrast, tidal flooding patterns among the created marshes were highly variable. Hydrologic differences can affect marsh use and habitat value in several ways (Rozas 1995). High-elevation marshes that are infrequently flooded, such as some of the created marshes in this study, are simply not available for direct exploitation by nekton to the extent of lower elevation marshes. Even when the marshes are flooded and fully accessible, however, our data indicate that flooding patterns affect nekton use, as evidenced by strong positive relationships between annual flooding durations and densities of many decapod crustaceans. In an experimental study, Minello et al. (1994) identified distance to the marsh/water interface (edge) and elevation as important factors affecting nekton densities on the surface of Marsh T1. Edge effects should have been minimal in our study because

no samples were farther than 5 m from the marsh/water interface. Our data, however, support the importance of surface elevation in determining the use of near-edge habitats by nekton. Rozas & Reed (1993) also documented differential use of marsh elevations by nekton in Louisiana; brown shrimp and white shrimp were concentrated in low-elevation marsh habitat.

When confronted with evidence of functional deficiencies in created wetlands, it commonly has been assumed that these wetlands will eventually develop into fully functioning habitats (Mitsch & Wilson 1996). This assumption has instigated searches for the slope and shape of developmental trajectories (Kentula et al. 1992, Richardson 1994, Simenstad & Thom 1996). Our created salt marshes ranged in age from 3 to 15 yr, thus we expected to see a general pattern of increased nekton use with marsh age. However, we found no obvious age-related patterns in use of the marshes by any nekton species examined. Sediment MOM increased with marsh age, but even this relationship was weak; age only explained 9% of the variability in MOM. These data may indicate that the time required to reach functional equivalency is very long, and trends cannot be observed within 15 yr. Or the data may indicate that some created salt marshes never reach functional equivalence with natural marshes (Sacco et al. 1994, Brinson & Rheinhardt 1996, Simenstad & Thom 1996). For nekton, we conclude that variability in use and in functional development rate is high in these created wetlands and that factors other than age are more important in determining habitat value. Marsh surface elevation appears to be a key characteristic influencing the value of created marshes for fishery species and estuarine nekton. Unless elevation changes occur

in the temporal development of a marsh, it appears unlikely that high-elevation created marshes will ever reach functional equivalency with natural marshes for these organisms.

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ERRATUM

Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA

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• Table 5 on page 176 contained incorrect italicisation and misplaced entries. The corrected table appears below.

Table 5. Stepwise multiple regression analyses on log-transformed densities of abundant fauna collected in drop samples using 8 independent variables: percent of time flooded over the year (FLOOD), sediment macro-organic matter (MOM), log-transformed abundance of sediment infauna (INF), sample water depth (DEPTH), salinity (SAL), water temperature (TEMP), dissolved oxygen (DO), and turbidity (TURB). The independent variable name is shown in italics if the relationship is negative. Data for each season are from all samples on the marsh surface (n = 57 in fall and 47 in spring). At each step of the analysis, the included variables are shown in order of their partial F-ratio in that model along with the adjusted R^2 value for the model; ns indicates that none of the variables contributed significantly to a model

Dependent variable	Independent variables					
	Step 1	R^2	Step 2	R^2	Final	R^2
FALL						
Total macrofauna	FLOOD	0.43	FLOOD MOM	0.47	FLOOD MOM DEPTH	0.51
Fishes	DEPTH	0.38	DEPTH *SAL*	0.43	DEPTH *SAL*	0.43
Gobiosoma bosc	DEPTH	0.26	DEPTH *SAL*	0.42	DEPTH *SAL* MOM	0.47
Gobionellus boleosoma	DO	0.23	DO FLOOD	0.27	DO FLOOD	0.27
Symphurus plagiusa	DEPTH	0.29	DEPTH TEMP	0.34	DEPTH TEMP	0.34
Sciaenops occellatus	DEPTH	0.18	DEPTH *SAL*	0.28	DEPTH *SAL*	0.28
Cynoscion nebulosus	DEPTH	0.38				
Decapod crustaceans	FLOOD	0.44	FLOOD MOM	0.49	FLOOD MOM DEPTH	0.52
Palaemonetes pugio	FLOOD	0.32				
Penaeus setiferus	*TURB*	0.28	*TURB* DEPTH	0.38	*TURB* DEPTH *INF*	0.42
Palaemonetes vulgaris	FLOOD	0.22	FLOOD *SAL*	0.37	FLOOD *SAL*	0.37
Palaemonetes intermedius	*SAL*	0.26	*SAL* FLOOD	0.39	*SAL* FLOOD	0.39
Callinectes sapidus	FLOOD	0.42	FLOOD *TURB*	0.46	FLOOD *TURB*	0.46
Clibanarius vittatus	FLOOD	0.14	FLOOD *DEPTH*	0.24	FLOOD *DEPTH* TEMP	0.36
Penaeus aztecus	*TURB*	0.38	*TURB* DEPTH	0.46	*TURB* DEPTH MOM DO INF	0.60
Molluscs						
Littoraria irrorata	ns				ns	
SPRING						
Total macrofauna	*SAL*	0.18	*SAL DEPTH*	0.25	*DEPTH* FLOOD	0.35
Fishes	ns				ns	
Brevoortia patronus	DEPTH	0.19	DEPTH *SAL*	0.25	DEPTH *SAL*	0.25
Lagodon rhomboides	DO	0.55	*DO TURB*	0.60	*DO* INF SAL *TURB*	0.71
Decapod crustaceans	*DEPTH*	0.14	*DEPTH* FLOOD	0.33	*DEPTH* FLOOD *TURB*	0.39
Palaemonetes pugio	ns				ns	
Penaeus aztecus	FLOOD	0.27	FLOOD *TURB*	0.37	FLOOD *TURB DEPTH*	0.47
Callinectes sapidus	*DEPTH*	0.33			*DEPTH*	0.33
Clibanarius vittatus	DO	0.26			DO	0.26
Molluscs						
Littoraria irrorata	ns				ns	